

Genetic Variation among Canada Wildrye Accessions from Midwest USA Remnant Prairies for Biomass Yield and other Traits

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ABSTRACT

Canada wildrye (*Elymus canadensis* L.) and Virginia wildrye (*Elymus virginicus* L.), which are native to the USA, were collected from remnant Midwest prairies. The objectives of this study were to determine the genetic variability among the collected accessions for biomass yield and other traits, determine the extent of genotype \times environment interactions for these traits across Midwest environments, and to determine the relationship between the geographical location of the collection site and evaluation sites for these accessions for plant biomass yield which can be used as a measure of adaptation. Seed collected from six Midwest states was bulked by collection site to form individual accessions. Space transplanted evaluation nurseries were established at Mead, NE, Ames, IA, and West Lafayette, IN, and accessions were evaluated on a plot basis for 2 yr. There was significant genetic variation among accessions for post-heading forage yield, heading date, height, pre-heading in vitro dry matter digestibility (IVDMD) and crude protein (CP) concentration, and post-heading CP concentration. Strain \times location (S \times L) interaction effects were only significant for post-heading IVDMD and height indicating that for the other traits, the relative ranking of the strains was similar at all three locations over the two evaluation years. Regression analyses of the effect of distance of the collection site from the evaluation site (direct, east or west, and north or south) on biomass yield were largely nonsignificant or had very low R^2 values. These regression results along with the nonsignificant S \times L effects from the analysis of variance indicate that longitudinal or latitudinal adaptation gradients for plant biomass yield are lacking for Canada wildrye accessions from Midwest prairies. All but five of the Canada wildrye accessions had higher biomass yield than the only released cultivar, Mandan, indicating that this germplasm can be used to develop improved cultivars that should be adapted to the region represented by the collection and evaluation sites.

THERE IS AN INCREASING DEMAND for the use of native plants in conservation and wildlife plantings throughout the USA. Many of the native grasses that have been used for these purposes have been warm-season C_4 grasses such as switchgrass (*Panicum virgatum* L.) and big bluestem (*Andropogon gerardii* Vitman). Most of the cool-season grasses that are used in the USA for forage, turf, and conservation plantings are introduced grasses such as tall fescue (*Festuca arundinacea* Schreb.)

and smooth brome grass (*Bromus inermis* Leyss.). The tallgrass prairie region of North America occupied over 500 000 km² of central North America in what is now the north-central states or Corn Belt region of the USA (Risser et al., 1981). Currently, only remnants of the original prairie remain.

Canada wildrye is a cool-season (C_3) grass that is native to most of the continental USA (Hitchcock, 1971; Barkley, 1986). It was one of the prevalent cool-season grasses in the tallgrass prairie region of the USA. It is a tetraploid species ($2n = 4x = 28$) and is largely self-pollinated (Sanders and Hamrick, 1980; Jensen et al., 1990). Virginia wildrye is another native cool-season grass that was found in most continental USA states except for California, Oregon, and Nevada (Hitchcock, 1971; Barkley, 1986). Virginia wildrye was typically found in moist, low ground along woods and streams. Canada wildrye has long awns (2 to 3 cm) while Virginia wildrye has short awns (about 1 cm in length) on their lemmas. Both species have the same number of chromosomes and are fertile when hybridized (Church, 1958). Hybrids between *E. canadensis* and *E. virginicus* have normal meiosis and produce viable, variable progeny (Church, 1958). Plants in native stands that resemble the hybrid progeny of *E. canadensis* and *E. virginicus* have been classified as *E. virginicus* var. *submuticus* Hook. or have been given other *E. virginicus* varietal designations (Hitchcock, 1971; Church, 1958; Barkley, 1986). These interspecific plants and populations have been found throughout the range of where the two species are found growing in association (Church, 1958; Pohl, 1959; Nelson and Tyrl, 1978).

To date, one cultivar each of Canada wildrye and Virginia wildrye has been released or developed. Mandan Canada wildrye was developed from collections made near Mandan, ND (Alderson and Sharp, 1994). Omaha wildrye is a privately developed Virginia wildrye cultivar that is produced by Stock Seed Farms, Murdock, NE. It originates from plant material collected in eastern Nebraska. Recently, accessions of Virginia wildrye originating in northeastern USA were evaluated at three locations in that region for forage yield, persistence, and plant morphology in space transplanted trials (Sanderson et al., 2004a). Two orchardgrass (*Dactylis glomerata* L.) cultivars and Omaha were included as checks. There were differences among wildryes for most traits depending on the year and location. The two orchardgrass cultivars outyielded the wildryes over years and locations and had better persistence. The forage quality of the Virginia wildrye accessions was similar to that of other cool-season grasses at similar stages of maturity (Sanderson et al., 2004b). The authors' conclusion was that the most viable

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Abbreviations: CP, crude protein; IVDMD, in vitro dry matter digestibility; PAR, Plant Adaptation Regions.

use for Virginia wildrye would be in conservation plantings rather than for forage purposes.

The tallgrass prairie region of North America is classified as the Prairie Parkland (Temperate) ecoregion province in the widely used ecoregion classification system developed by Bailey (1995, 1997, 1998). Vogel et al. (2005) overlaid Bailey's ecoregion province classification system with the USDA Plant Hardiness Zone Map (Cathey, 1990) to develop Plant Adaptation Regions (PAR) which integrate the ecological and climatic variables that affect plant adaptation in a region.

Canada wildrye and Virginia wildrye accessions were collected from remnant prairies in this region in the autumn of 1989 (Vogel et al., 1992). The objectives of this research were to determine the genetic variability among the collected accessions for agronomic traits, determine the extent of genotype \times environment interactions for these traits across Midwest environments, and to determine the relationship between the geographical location of the collection site and evaluation sites for these accessions for plant adaptation as measured by biomass yield. Plant biomass yield or plant size has been used in ecological studies as a measure of plant adaptation to a site (Byers, 1998; Montalvo and Ellstrand, 2001; Gustafson et al., 2004). Plant Adaptation Regions will be used in this report to describe both the wildrye accession's collection and evaluation sites.

MATERIALS AND METHODS

In this report, *site* refers to the area from which the seed was collected, *location* refers to the three areas where the evaluation trials were transplanted, and *strain(s)* refers to the

individual accessions or cultivars that were included in the research. Strains identified as ACMO, HCMO, and MO followed by a number were from Missouri. The first two letters of the strain designation is the postal code for the state origin of the remaining strains. Within a state, accessions were designated by the numerically coded site from which they were collected, for example, accession NE3 was from Nebraska prairie site 3.

Seed was collected from Canada wildrye plants and from plants of nonbearded Virginia wildrye plants that phenotypically were similar to the botanical description of *E. virginicus* var. *submuticus*. These are described in this report as the Canada wildrye (C) or Virginia wildrye (V) phenotypes. The collections were made in the autumn of 1989 from remnant prairie sites (Fig. 1, Table 1) in the north-central USA (Vogel et al., 1992; Hopkins et al., 1995; Vinton et al., 2001). The accession IL62 was collected from a restored prairie planted in 1940; all other accessions originated from unplanted, native prairie sites. The collection sites are representative of the remnant prairie sites that exist in the region. At each site, spikes were collected from throughout the remnant site in a random manner. Seed from all the spikes from a site were bulked and threshed. Bulk seed was given an accession number that identified both the accession and the collection site.

Seed from each accession was wet chilled for 3 wk at 4.5°C and planted in the greenhouse into plastic seedling tubes (22 cm deep and 4 cm in diameter) which contained a mixture of 2:1:1 soil/peat/vermiculite. After emergence, seedlings were thinned to one seedling per tube. Seedlings of the accessions and the check cultivar Mandan Canada wildrye were transplanted into single-row plots at the three field evaluation sites which were near Mead, NE, Ames, IA, and West Lafayette, IN. Soil type was Sharpsburg silt loam (fine, smectitic, mesic Typic Argiudoll) at Mead, Webster silty clay loam (fine-loamy, mixed, superactive, mesic Typic Endoaquoll) at Ames, and Xenia silt loam (fine-silty, mixed, superactive, mesic Aquic Hapludalf) at West Lafayette. Climatic conditions at the three sites for the

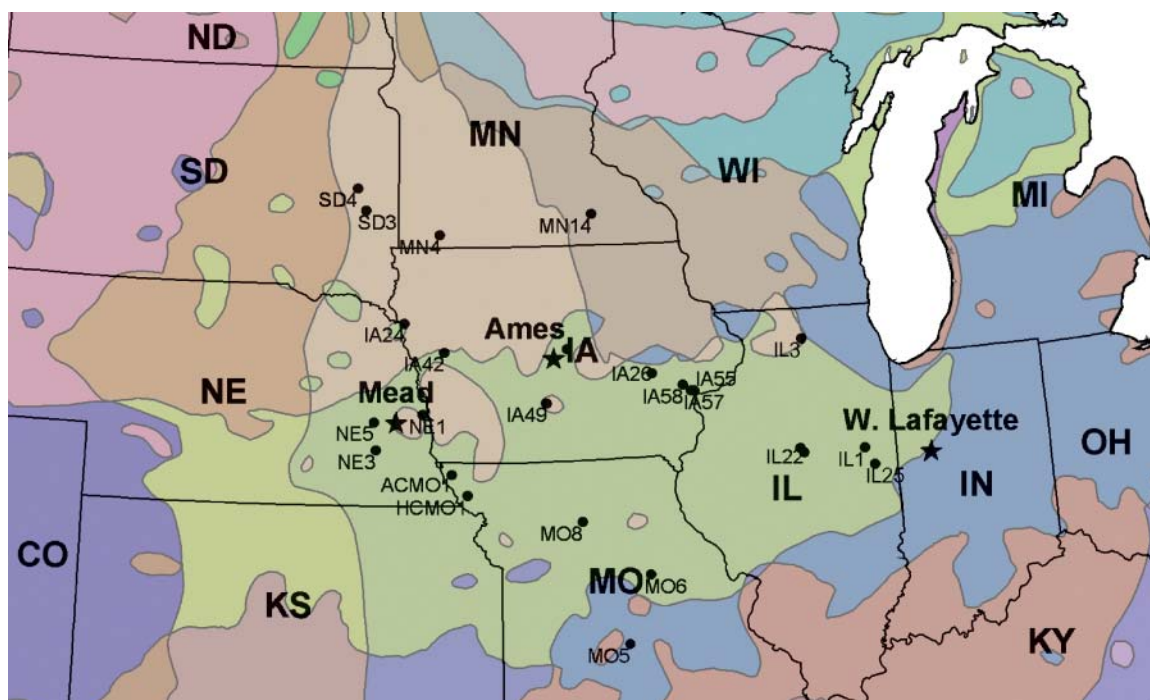


Fig. 1. Plant Adaptation Regions (colored regions), Canada wildrye collection sites (•), and evaluation locations (star) for Canada wildrye accessions collected from remnant Midwest prairies. Plant Adaptation Regions are: light green, PAR 251-5 (Temperate Prairie Parkland, Plant Hardiness Zone 5); tan, PAR 251-4; light brown, PAR 222-4 (Eastern broadleaf forest, Plant Hardiness Zone 4); blue, PAR 222-5.

Table 1. Canada and Virginia wildrye accession or strain means averaged over three Midwest locations (Mead, NE, Ames, IA, and West Lafayette, IN) for biomass yield and other traits.

Strain	Type†	Yield g plant ⁻¹	Heading date DOY‡	Spike height cm	Pre-heading		Post-heading	
					IVDMD‡	CP‡	IVDMD	CP
					g kg ⁻¹			
ACMO1	C	676	201	130	651	144	497	93
ACMO1L	C	671	179	138	599	152	474	86
HCMO1	C	455	197	122	699	159	508	97
MO5	C/V	141	183	90	645	172	451	108
MO6	C	117	189	101	644	162	451	110
M06A	V	259	184	88	623	157	456	105
MO8	V	330	182	111	614	151	429	99
IA24	C	608	200	134	690	166	496	100
IA26	C/V	335	190	98	636	168	481	110
IA42	C	646	198	126	676	161	498	97
IA49	C	431	197	132	700	158	465	96
IA50A	V	403	189	79	653	158	497	96
IA55	C	241	182	98	640	165	461	104
IA57A	V	374	188	104	620	157	481	113
IA58	C/V	465	191	134	659	162	489	90
MN14	C	464	197	110	671	168	499	100
MN4	C	472	193	94	711	167	488	100
IL1	C	488	190	110	651	160	454	91
IL21	C/V	527	202	96	655	182	526	121
IL22	C	498	196	124	681	179	498	103
IL25	V	223	189	74	660	159	482	112
IL 3	C	469	176	117	654	153	475	93
IL62	C	565	193	130	682	163	514	96
NE1	C	463	196	118	668	149	478	93
NE3	C	484	190	125	667	151	487	97
NE5	C	517	186	124	660	154	482	94
SD3	C	160		70	667	234	504	123
SD4	C	390	190	92	707	192	559	117
Mandan	C	286	179	103	677	172	489	107
LSD 05		225	11	18	56	17	ns	15
Means								
Overall		431	190	111	661	163	485	101
Ames, IA		322	190	104	597	129	459	98
Mead, NE		401	194	109	676	174	472	95
W. Lafayette, IN		566	188	120	711	184	522	110

† C, *E. canadensis* accession; V, *E. virginicus* accession; C/V, accession contained both types.

‡ DOY, day of the year; IVDMD, in vitro dry matter digestibility; CP, crude protein.

duration of the trial are summarized in Table 2. The experimental design was a randomized complete block (RCB) with two replicates or blocks at each location. A plot consisted of a single row of 10 plants at Mead and Ames and 7 plants at West Lafayette. Plants within a row and rows were spaced 1.1 m apart.

During the establishment and post-establishment years, herbicides and hand weeding were used for weed control and the nurseries were essentially free of weeds. The herbicides, rates, and application dates varied with location and year but typically included herbicides for pre-emergence control of both

grassy and broadleaf weeds that was applied in the spring each year. The nurseries were fertilized with 112 kg ha⁻¹ N as ammonium nitrate in April or early May of 1991 and 1992 at each location. No fertilizers were applied the establishment year.

No data were collected during the 1990 establishment year. The plots were evaluated for stands, biomass yield, heading date, spike height, and forage quality traits in 1991 and 1992. Stand data were obtained by counting the number of surviving plants in a row. Heading date was the date on which the majority of the plants in a plot had three or more heads exerted from the flag leaf. Accessions were identified as having the C or V phenotype before forage harvest by the senior author. Vegetative samples were collected before heading in late April or May at each location while post-heading samples were collected just before forage biomass harvest in July or early August. Post-heading samples and harvests at the West Lafayette site were collected as plants headed, while at Mead and Ames the samples were collected and forage harvests were made after all accessions in the nurseries had headed. At both sampling periods, samples were collected by cutting three to four tillers, at approximately 10 cm of height, from each plant within a plot. Samples were dried in forced-draft ovens at 50°C (60°C at West Lafayette) to determine dry matter concentration of the samples which were used to adjust forage biomass yields to a dry weight basis. Plots were harvested at a height of 10 cm using a flail plot harvester. The dry weight of the forage samples collected for dry matter and quality analysis was added to the plot forage yield. The number of plants in each plot at harvest was determined and forage yield was expressed

Table 2. Climatic data, with deviations from average, for the 1991 and 1992 growing seasons at Mead, NE, Ames, IA, and West Lafayette, IN.†

Location	Seasonal precipitation		Monthly temperature	
	Total	Deviation	Average	Deviation
cm				
°C				
1991				
Mead‡	58.9	-9.3	18.9	0.3
Ames	75.3	9.9	18.0	0.7
West Lafayette	51.4	-13.9	19.1	1.5
1992				
Mead	42.0	-20.0	17.5	-2.2
Ames	55.9	-3.6	17.0	-1.4
West Lafayette	63.4	4.6	16.9	-1.5

† Growing seasons were April to October 1991 and April to September 1992.

‡ Nearest reporting stations with complete precipitation (Wahoo, NE) and temperature (Ashland, NE) data were used for Mead.

as dry weight per plant by dividing plot yield by the number of harvested plants per plot. This was necessary because some seedlings died after transplanting in the establishment year. Stands were stable at all three sites after the establishment summer. Subsequent stand losses were so minimal that analysis for stand losses was not conducted.

Forage Quality Analyses

The dried forage samples were ground in a Wiley shear mill to pass a 1-mm screen and reground to uniformity in a cyclone impact mill. All samples were scanned using a near infrared reflectance spectrophotometer (NIRS; Technicon Infralyzer 500, Bran & Luebbe Analyzing Technologies, Buffalo Grove, IL) over a wavelength range of 1100 to 2500 nm with 2-nm steps. Development and verification of prediction equations for IVDMD on wet lab values were as described by Hopkins et al. (1995). Crude protein concentration ($N \times 6.25$) was determined by the University of Nebraska Agronomy Department Analytical Laboratory using the Kjeldahl procedure. NIRS prediction equations were developed for forage protein concentrations using the same NIRS calibration procedures as for IVDMD. The prediction equations for IVDMD and CP had R^2 values of 0.96 and 0.94, respectively and the standard error of calibration (SEC) was 2.13 and 1.06, respectively, for the two traits.

Statistical Analyses

Because the wildrye accessions were perennials, data were analyzed across years as a split plot in time with strains as whole plots, years as split plots, and blocks nested within locations (Hicks, 1973). Populations or strains were considered to be fixed effects and years, replications, and locations were assumed to be random effects. The method of Neter et al. (1985) was used to calculate approximate F values and approximate degrees of freedom were calculated according to Satterthwaite (1946). Regression analysis was conducted to determine if the distance of the collection site from the evaluation site had an effect on individual plant biomass yield. A Cartesian grid was placed over a map on each of the three evaluation sites and the distance north (+), south (-), east (+), or west (-) of the collection site from the evaluation site was determined. Regression analysis was done for the effect of direct distance, north or south distance, and east or west distance on individual plant biomass yield. This analysis was completed using only Canada wildrye accessions from sites known to be true remnant prairies (Fig. 1). All data were analyzed using SAS software (SAS Institute, 1999).

RESULTS AND DISCUSSION

The wildryes evaluated in this report were largely collected from Plant Hardiness Zones 4 and 5 of the temperate Prairie Parkland ecoregion province (PAR 251-4 and PAR 251-5, respectively) although two accessions, MN14 and MO 5, were collected from PARs 222-4 and 222-5 (Eastern Deciduous Forest, Hardiness Zones 4 and 5, respectively; Fig. 1). The evaluation site at Mead, NE, is in the western part of the Prairie Parkland ecoregion province and is on the boundary of Plant Hardiness Zones 4 and 5. The West Lafayette site is on the boundary of the Prairie Parkland and Eastern Deciduous Forest provinces and is in Plant Hardiness Zone 5. The Ames, IA, site is typical of the Prairie Parkland

province and is in Plant Hardiness Zone 5. The environmental conditions during the evaluation period at the three locations were representative of the environmental variation that exists in the temperate Prairie Parkland ecoregion over years (Table 2). Annual precipitation was substantially below the long-term average in both 1991 and 1992 at Mead, NE, and in 1991 at West Lafayette. Precipitation at Ames in 1991 was almost 10 cm above normal. Temperatures were somewhat warmer and cooler than normal, respectively, in 1991 and 1992 at the three locations.

Accessions that were evaluated included both C and V phenotypes (Table 1). The V phenotypes were almost entirely similar to the plants produced by hybridization of Canada wildrye and Virginia wildrye and described botanically as varieties of Virginia wildrye (Hitchcock, 1971; Church, 1958; Barkley, 1986). Because they were found growing in proximity with the Canada wildryes and since they were likely part of the wildrye germplasm complex at a prairie site, the Virginia wildrye strains were included in the evaluation trials with true Canada wildrye strains.

There was significant variation among accessions or strains when evaluated over years and evaluation sites for forage biomass yield, heading date, height, pre-heading IVDMD, and protein concentration (Tables 1 and 3). Strain \times location interaction effects were not significant for forage biomass yield, heading dates, pre-heading IVDMD, or protein concentration. This indicates that the relative values of the strains were similar at all three locations over the two evaluation years for these traits. There were significant strain \times location interaction effects for post-heading IVDMD which were probably due to the West Lafayette samples being collected as strains matured while the samples at the other two sites were all collected at a single harvest date. There were significant strain \times location interaction effects for height but the mean square for the strain effect was 10 times that of the strain \times location effect and the σ^2 for strains was about 5 times the σ^2 for strains \times locations (data not shown) indicating their relative importance. Because strain \times location effects were not significant for most traits or of minor importance, only over-location means are reported.

Some of the collected accessions contained mixtures of plants with the C or V phenotypes. These strains and the strains that were classified as *E. virginicus* or V phenotypes were within the range of means for forage biomass yield, digestibility, and crude protein content of the Canada wildrye strains both when compared to all accessions and to accessions collected in the same state. The Virginia wildrye accessions typically were shorter in stature than the Canada wildrye accessions. In production agriculture, the only apparent merit that the *E. virginicus* accessions would have in comparison to Canada wildrye accessions is that their short awns would make seed harvest and processing easier.

There were significant differences among accessions over locations for biomass yield which was consistent over all test locations (Table 3). All but five of the accessions had higher biomass yield than the Canada wild-

Table 3. Mean squares from the analysis of variance for biomass yield and other traits for Canada and Virginia wildrye accessions or strains collected from remnant Midwest USA prairies and evaluated at three Midwest sites.

Source	df	Biomass yield	Heading date	Height	Pre-heading		Post-heading	
					IVDMD†	CP†	IVDMD	CP
		g plant ⁻¹	DOY†	cm	g kg ⁻¹			
Location	2	1 640 231	1241	7932	327 980	83 830	112 820	6280
Strain	28	199 738	531	3873	8600	1420	7001	840
Replicate (L)‡	3	207 016	79	173	8350	600	1480	320
L × S†	54	49 380	140	389	2440	260	2330	180
S × R (L)‡†	80	19 663	108	89	1780	140	1130	180
Year	1	11 771	14 780	27 248	176 840	230	456 420	5260
L × Y‡	2	561 899	554	7675	243 840	25 790	35 660	5460
Y × R (L)	3	4109	118	16	3220	70	2460	40
S × Y	27	50 891	154	200	3650	330	3420	300
L × S × Y	53	26 521	112	126	1500	170	1090	140
Error	69	13 527	115	65	1800	150	1320	160
F for strain		2.71**	2.92**	8.37**	1.87*	3.38**	1.50	2.47**
F for S × L		1.51	1.33	2.59**	1.65	1.63	2.59**	1.13
F for S × Y		1.92*	1.38	1.59	2.43*	1.94*	3.15*	2.14**

* Indicates significance at the 0.05 level of probability.

** Indicates significance at the 0.01 level of probability.

† IVDMD, in vitro dry matter digestibility; CP, crude protein; DOY, day of the year.

‡ L, location; S, strain; R, replicate; Y, year.

rye cultivar Mandan that was included in the study as a control. Because of the stability for yield of Canada wildrye strains across the broad evaluation area, it should be feasible to use the highest yielding accessions to develop new cultivars of Canada wildrye for use in the PARs 251–4 and 251–5 that will be superior to Mandan. The difference in pre-heading IVDMD and crude protein concentration among strains may be influenced by differences in maturity but this cannot be tested because we did not stage the plants for maturity when the vegetative samples were collected. There were no significant differences among strains for IVDMD when post-heading samples were analyzed. Based on the range in values, heritable differences among the wildrye accessions for IVDMD likely exist but it will take additional trials with more replicates to identify strains with high IVDMD. Significant differences in CP concentration existed among strains at both harvests suggesting that it should be feasible to develop Canada wildrye cultivars with improved crude protein concentration.

Regression analysis was used to determine the relationship between distance of the collection site from the evaluation site and accession biomass yield. There were no significant effects of direct distance of the evaluation site from the collection site for the three evaluation sites (Table 4). The north to south and east to west distance of the evaluation site from the collection site were not significant for either Mead, NE, or West Lafayette, IN. There were significant differences for north to south and east to west distances of the collection site from the evaluation site for the Canada wildrye accessions evaluated at Ames, IA, but the regression equations had relatively low R^2 values indicating low predictability. Based on the sign and magnitude of the regression coefficients (b values), the farther north a strain was collected from Ames, the higher its yield was at Ames and opposite for strains originating south of Ames (Table 4). The farther west an accession was collected from Ames, the higher its yield was at Ames and the opposite for strains collected east of Ames. The effect of distance of collection site distance

from Ames ranged from 0.28 to 0.44 g km⁻¹ which is very small considering the magnitude of differences for biomass yield.

The regression results demonstrate that although Canada wildrye accessions from Midwest prairies differ significantly for biomass yield, there is a low or nonsignificant association between germplasm origin and test site location for biomass yield over a broad geographical area. These regression results are supported by the over-locations analysis of variance that showed that strain × location effects were not significant for biomass yield. These results indicate that Canada wildrye accessions from Midwest Prairies are adapted to a broad geographical area and the best plant material can be used throughout the region represented by the collection and evaluation sites.

The utility of improved strains of Canada wildrye in grassland production systems in the Midwest will need to be determined in sward trial comparisons with smooth brome grass and other cool-season grass cultivars currently being used in the region for pastures. A portion of the Canada wildrye accessions were evaluated in space transplanted seed increase nurseries for the presence of endophytic fungi (genus *Neotyphodium*) by Vinton et al.

Table 4. Regression statistics for the regression of biomass yield (g plant⁻¹) on the distance and directional distance between evaluation locations and collection sites for Canada wildrye germplasm accessions collected and evaluated in the Midwest, USA.

Distance type†	Statistic‡	Mead, NE	Ames, IA	W. Lafayette, IN
Direct vector	R^2	0.05	0.05	0.04
	b	-0.14	-0.25	0.18
North-south	R^2	0.05	0.26*	0.09
	b	0.19	0.44*	0.40
East-west	R^2	0.02	0.19*	0.05
	b	-0.07	-0.28*	-0.21

* Indicates significance at the 0.05 level of probability.

† North to south and east to west distance is the distance (km) north (+), south (-), east (+), or west (-) of the collection site from the evaluation site; direct vector is the distance between evaluation and collection site.

‡ $n = 23$ for each site.

(2001). The endophyte was found in all of the accessions that were evaluated. The effect of the endophyte on ruminants will need to be determined in grazing trials if Canada wildrye appears to be competitive with brome-grass and orchardgrass in the sward trials. The use of Canada wildrye in conservation plantings will continue but these results indicate that broadly adapted cultivars can be used for these plantings in the Midwest. Virginia wildrye strains may be useful in increasing the botanical diversity in conservation plantings.

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